

Spatial analysis of the habitat and distribution of *Osmoderma eremita* (Scop.) in trees outside of woodlands

Benoît Dodelin¹, Simon Gaudet², Guillaume Fantino³

1 11 rue Montesquieu; 69007 Lyon, France **2** Parc naturel régional des Boucles de la Seine Normande - Maison du Parc; 76940 Notre-Dame-de-Bliquetuit, France **3** Geopeka - École Normale Supérieure de Lyon; 46 Allée d'Italie - Bât. LR6; 69364 Lyon Cedex 07, France

Corresponding author: Benoît Dodelin (benoitdodelin@orange.fr)

Academic editor: S. Hardersen | Received 24 February 2017 | Accepted 9 June 2017 | Published 31 July 2017

<http://zoobank.org/8AE23352-ADCC-4405-933C-3146D211364E>

Citation: Dodelin B, Gaudet S, Fantino G (2017) Spatial analysis of the habitat and distribution of *Osmoderma eremita* (Scop.) in trees outside of woodlands. In: Campanaro A, Hardersen S, Sabbatini Peverieri G, Carpaneto GM (Eds) Monitoring of saproxylic beetles and other insects protected in the European Union. Nature Conservation 19: 149–170. <https://doi.org/10.3897/natureconservation.19.12417>

Abstract

The endangered and specialised saproxylic beetle *Osmoderma eremita* occurs in veteran trees, a habitat particularly threatened by changes in agricultural landscapes. Its conservation requires information about populations and key features of host trees. Surveys of 8,014 trees (pollarded or in hedgerows) were carried out and analysed, based on habitat description (tree level) and spatial information (hedgerow length and distance to the nearest inhabited tree). A suitable cavity was present in 61% of the trees and *O. eremita* was detected in 42 trees, mainly in *Salix* (30 observations), the most common tree amongst those surveyed. A small or absent crown was a significant factor in explaining the beetle's presence, as was the distance to the nearest inhabited tree. The largest population of *O. eremita*, 19 inhabited trees, was found in a wide and continuous area formed by trees with suitable cavities, with distances of less than 250m from each another. Seven smaller areas, with 7, 5 or 1 inhabited trees, were also found. When analysing inhabited trees on a 1km² grid, 17km² hosted *O. eremita*, corresponding to a dense network of 63km of hedges. The presence of *O. eremita* significantly increased per km² with increasing length of hedges and this variable was thus used to guide forthcoming investigations directed toward *Osmoderma*. As the hedgerows existing in 1999 had decreased by 6.1% in 2009, it is concluded that the long term survival of *O. eremita* is under threat. The preservation of trees outside woodlands is urgent and has already started, in connection with Natura 2000 policies. Regeneration and creation of new hedgerows is also ongoing and can be reinforced both by using *Salix* and by promoting pruning to increase formation of cavities.

Keywords

Insect conservation, Habitat quality, *Osmoderma eremita*, Saproxylic beetle, Hollow tree

Introduction

Wood pastures, hedgerows with trees and trees outside woodlands (TOW) (Alexander et al. 2016) are known to host an important biodiversity, including specialists, threatened, rare and protected species (Vallauri et al. 2005, Fayt et al. 2006, Stokland et al. 2012, Ramírez-Hernández et al. 2014), as well as species useful for agriculture (Burel et al. 2004). Specialists are mostly represented by saproxylic species i.e. “organisms involved in or dependent on the process of fungal decay of wood, or on the products of that decay and which are associated with living as well as dead trees” (Alexander 2008). *Osmoderma eremita* (Scopoli, 1763) (Coleoptera, Scarabaeidae), the hermit beetle, is a member of these saproxylic species, endemic to Western Europe (Audisio et al. 2007). It is listed as Near Threatened in the European IUCN Red List. The species strictly depends on veteran trees, as it inhabits decaying heartwood inside tree hollows, a very specific habitat type which is already highly fragmented and subject to a significant and continuing decline in Europe (Nieto et al. 2010). *O. eremita* is vulnerable to habitat fragmentation (e.g. Ranius and Hedin 2001) and is considered a relict species of primeval forests (Müller et al. 2005). It is also listed in Appendix II of the Bern Convention and is strictly protected in Europe as a priority species in Annexes II and IV of the Habitat Directive 92/43/EEC. EU member States are thus required to protect, manage and monitor the habitat of *O. eremita*, in accordance with the ecological needs of the species. In France, this is done via both national and regional strategies for biodiversity (MEDDE 2012). Diverse operational tools are used, such as strict protection by law, delimitation of ecological corridors, regional plans for ecological coherence and the Natura 2000 network. In France, the most recent evaluation of the conservation status for *O. eremita* is U2: Unfavourable-Bad (Bensettiti and Puissauve 2015). Indeed, important populations continue to be threatened by planning decisions (e.g. Dirksen and Mériguet 2009).

In the northwest of France, a dense hedgerow network persisted over centuries in connection with the traditional system of agriculture. The maximum density of the hedgerow network was reached at the end of the 19th century and decreased from the 1950s onwards, mainly as a result of intensified farming practices (Burel and Baudry 1990, Dubois et al. 2009). In the context of attempts to preserve the remnants of this network, *O. eremita* represents an umbrella species, a species whose conservation is expected to confer protection on a large number of other naturally co-occurring species (Roberge and Angelstam 2004). Protecting *O. eremita* can help to build conservation policies for hedgerows with trees and TOW and can also facilitate the raising of public awareness for relevant conservation issues (Luce 2001).

The Parc Naturel Régional des Boucles de la Seine Normande (PNR-BSN) is partly covered by a dense and extensive network of large trees following the Seine river.

This area is also characterised by the presence of two large cities, Rouen and Le Havre. The Seine river, with the major ports of Rouen, Le Havre and Paris, is economically important. This context negatively impacts wetland ecosystems: dredging, drainage and gravel mining are common activities and today, this last activity probably has the most significant negative impact on old trees as it is often carried out inside the hedgerow network. Conflicts between nature protection and economic development are thus a serious problem. Moreover, historic data collected before 1950 suggested that *O. eremita* could be present in the hedgerow network. The PNR-BSN hence decided to use this species as an indicator of the quality of the network. In accordance with the state services (DREAL), this was integrated into the objectives and action plans of Natura 2000 sites, as well as into the PNR-BSN conservation strategy for 2012–2016 (Gaudet 2013). Three years of research and inventories have yielded numerous data, which the present study will analyse.

The specific aims of this study are to:

- a) contribute to the knowledge on the ecology of *O. eremita*;
- b) explore the characteristics of the inhabited trees and their spatial patterns in the hedgerow network in the PNR-BSN;
- c) predict favourable areas where *O. eremita* is likely to occur and contribute to the establishment of guidelines for actions favourable for the protection of the species.

Material and methods

Ethics statement

This study is based on fieldwork carried out with prefecture permits dated 19/08/2008 (fieldwork from summer 2008 and earlier) and 30/07/2013 (fieldwork from 2013 to 2016).

Species studied

Until recently, European *Osmoderma* were considered as a single species, *O. eremita* (Scopoli, 1763), but recent evidence regarding morphology and from sequencing of mtDNA cytochrome C oxidase I gene, leads to a division into two distinct lineages. West European populations belong to *O. eremita* and the eastern ones to *O. barnabita* Motschulsky, 1845, while in Southern European ancient glacial refuges, there are three others species: *O. italicum* Sparacio, 2000, *O. cristinae* Sparacio, 1994 and *O. lassallei* Baraud & Tauzin, 1991, respectively endemic to the Italian peninsula, Sicily and Greece and European Turkey (Sparacio 2000, Ranius et al. 2005, Audisio et al. 2007, 2009, Landvik et al. 2013, Zauli et al. 2016).

Osmoderma species live in the cavities of large and old broad-leaved trees and, very likely, they all have the same biological requirements. Suitable trees can be in

old-growth forests (Luce 1995, Chittaro and Sanchez 2015) or outside woodlands, especially in wooded pastures, hedgerows (Vignon 2008), rural avenues and old parks around and inside cities (Oleksa et al. 2007, Blanc 2012). A female lays an average of 40 eggs. Larvae live in wood mould created by heartwood fungi (red rot formed mostly by *Laetiporus sulphureus* (Bull.) Murrill or *Fistulina hepatica* (Schaeff.) With.). They develop for 2 to 3 years, depending on the conditions in the cavity, e.g. mainly hygrometry and nutriment quality (Tauzin 2005) and the presence of microbial activity (Landvik et al. 2016a). An average mortality during the nymphal stage of approximately 25% has been observed (Tauzin 2005).

In Sweden, Ranius and Hedin (2001), observed only a low proportion (15%) of beetles dispersing from their natal tree. In contrast, in Italy, smaller populations per tree have been found and dispersing adults are exposed to a high predation rate (at least 28%) (Chiari et al. 2013). According to this study, 39% of dispersing individuals reached distances of greater than 250m. Generally dispersal abilities of the hermit beetle are very low, of the order of a few hundred metres. Radio-tracking yielded maximum flight distances of 180m (Hedin et al. 2008), 700m (Dubois and Vignon 2008) and 1,504m (Chiari et al. 2013). Other techniques confirmed this range of dispersal: 190m (Ranius and Hedin 2001) and 2,090m (Valainis et al. 2015) with mark-recapture studies, about 500m calculated with DNA markers (Oleksa et al. 2013) and a maximum single flight distance of 1,454m and a maximum cumulative flight distance of 2,361m obtained with a flight mill (Dubois et al. 2010). Dispersal is probably guided by the (R)-(+)- γ -decalactone, a pheromone emitted by males to attract females and sometimes also males in various other species of *Osmoderma* (Larsson et al. 2003, Svensson et al. 2009, Zauli et al. 2016).

In France, although *O. eremita* is widely distributed, a large proportion of the known localities are old or very old and many local populations are already extinct (Tauzin 2005). Currently, the largest populations are in the western part of the country, the south of the Massif-Central and around the Mediterranean sea, where hedgerow networks formed a continuous habitat before 1950 (Muséum national d'Histoire naturelle 2003, Vignon 2008). In the PNR-BSN, the first and only historical record is prior to 1950 and it concerns the plateau of Barneville-sur-Seine and Caumont, in south-east PNR-BSN. No other local information about the species was known prior to the intensive investigations started in 2005 (Vignon and Dubois 2005, Simont and Dufrêne 2007, ALISE Environnement et al. 2008).

Study area

Fieldwork was carried out in the territory of the PNR-BSN, North-West of Paris, France (49°27'03"N; 00°39'57"E). In this area, hedgerows and orchards still form a dense network in areas such as the Seine and Risle valleys, the Marais Vernier and the southern plateau. The territory of the PNR-BSN has not been studied exhaustively. Based on aerial photographs, study sites were selected that included a dense network

of hedges with trees and pollarded trees. In 2007, the studied area covered the Seine river floodplain at the meanders of Jumièges, Anneville/Ambourville, Roumare and the Roumois' plateau. In 2008, the survey investigated the western part of the PNR-BSN, the Roumois' plateau, the meander of Brotonne, the Marais Vernier and the Risle valley. Selected sites were studied exhaustively: all suitable trees within each site were surveyed (woodlands excluded).

Field search of *Osmoderma*

The field inventory of trees was undertaken during summer and autumn 2005-2015, with most work being done in 2005 and 2007-2008. Over the period from 2012-2015, trees inhabited by *Osmoderma* or with indices of presence were surveyed (see below) in order to confirm the activity of the species. Altogether, 8,014 trees were investigated (Table 1).

If necessary, ladders (length 4m) were used to reach the trunk cavities. A total of 38 cavities were unreachable. Cavities were explored visually with a lamp and their depth was estimated with a small diameter metal rod. The surface of the wood mould was inspected in order to search for indications of the presence of *Osmoderma*, those indications being live larvae and imagines, cocoons made with wood mould, remains of exoskeleton and/or larval faecal pellets. When no indications were observed on the surface, a small amount (approximately 1 litre) of wood mould was sieved and spread out on a white sheet in the field for careful inspection. Afterwards, the wood mould was returned to the cavity. The characteristic odour of the male pheromone was also considered as indicating the presence of *O. eremita*.

The detection of *Osmoderma* in cavities may be difficult and increasing the sampled volume of wood mould increased the probability of detecting larvae (Chiari et al. 2014). A volume of up to 8 litres of wood mould per tree was retained by Ranius and Jansson (2002). Here a compromise was adopted between the desire to survey a large number of trees and the volume of wood mould investigated per tree. As indices of presence can endure for a long time in a cavity, especially in dry conditions, only direct observation of live larvae, nymphs and imagines are proof of the actual presence of *Osmoderma* in a cavity (Dubois 2009). However, the presence of remains of exoskeletons is strongly correlated with an actual population (Ranius and Jansson 2002). In this study, it was decided to classify a tree as a host of *O. eremita* if live individuals (larvae and/or imagines) were seen or if cocoons, remains of exoskeletons or abundant amounts of faecal pellets were observed.

Tree and environmental variables

During the field work, spatial coordinates of each tree were taken with a GPS. Trees were described and cavities examined. The trees descriptors were: identification to spe-

Table 1. Data sources and description for *Osmoderma eremita* in the PNR-BSN. Some trees have been surveyed two times or more.

Year of sampling	Type of survey	Trees surveyed	Trees inhabited by <i>Osmoderma eremita</i>	Reference
2005	Targeted searches (Scale: tree patch)	4,181	8	(Vignon and Dubois 2005)
2007	Full inventory (Presence-Absence data)	4,378	29	(Simont and Dufrêne 2007)
2008	Full inventory (Presence-Absence data)	3,608	2	(ALISE Environnement et al. 2008)
2012	Targeted searches (Scale: tree)	5	4	PNR-BSN
2013	Targeted searches (Scale: tree)	383	10	PNR-BSN
2014	Targeted searches (Scale: tree)	31	22	PNR-BSN
2015	Targeted searches (Scale: tree)	2	2	PNR-BSN
Total		8,014	42	This study

cies level, evolution stage of hollow defined according to Ranius et al. (2001) and which incorporates an estimate of the volume of the cavity and of the wood mould, date of last pruning, size of the tree crown.

All tree variables were pair-tested to confirm the absence of correlations. Values of large discontinuous variables were then grouped into smaller categories to reinforce the explanatory powers of the models: the information on tree species was reduced to the three most common genera plus a fourth category which contained all other genera; the developmental stage of the cavity was grouped into three categories instead of five; crown development was reduced to three categories instead of five (Table 2).

Hedgerows with trees were measured using the 1:2,000 and 1:5,000 maps of the PNR-BSN. Ortho-photographs from 1973, 1999 and 2009 were digitalised and classified according to hedgerow types, amongst which were selected only hedgerows composed of trees or containing trees with a minimum length of 15m (forest edges excluded). Solitary trees, small series of pollards and orchards were also included. In this article, the terminology tree outside woodland (TOW) was used to refer to a hedgerow with trees together with solitary and/or pollards and orchards.

Connectivity was measured in two ways. First, the distance to the nearest neighbour tree inhabited by *O. eremita* was used. There is evidence that this measure is less powerful (Moilanen and Nieminen 2002, Buse et al. 2016), for it ignores the numerous sources of colonisation in the landscape (Prugh 2009). Second, the length of TOW per 1 km² was used, a buffer measure within a limited neighbourhood of the focal TOW, with no effect on distance. This measure was expected to have more explanatory power (Moilanen and Nieminen 2002, Prugh 2009, Ranius et al. 2010).

The landscape context of TOW was described by considering groups of trees at the 250m spatial scale. Groups were constructed by applying a buffer zone around any tree having a suitable cavity (i.e. cavity of stage 2, 3 or 4) and then by merging the adjacent polygons. The areas of the resulting zones (in hectares) were then calculated, the number of trees counted and the length of hedges contained in these polygons.

Table 2. Description of Variables.

Variable	Description	Categories used in models
Tree genera	<i>Salix</i> (n = 3,961). <i>Fraxinus</i> (n = 2,227). <i>Populus</i> (n = 1,286). <i>Carpinus</i> (n = 185). <i>Quercus</i> (n = 74). Other trees + Missing data (n = 281).	<i>Salix</i> (n = 3,961). <i>Fraxinus</i> (n = 2,227). <i>Populus</i> (n = 1,286). Other (n = 540).
Developmental stage of cavity	Stage 0: no cavity (n = 576). Stage 1: beginning of cavity development, not deep, small amount of mould (n = 2,157). Stage 2: Cavity with mould and a small entrance (n = 1,125). Stage 3: Large cavity with an important volume of mould (>5 litres) and a small entrance, optimum stage for <i>Osmoderma</i> (n = 1,067). Stage 4: Large and open cavity, empty of its mould after natural degradation of the trunk. The cavity soon to be uninhabitable by <i>Osmoderma</i> (n = 2,711). Stage 5: Dead or alive tree with emptied cavity (n = 373). Missing data (n = 5).	Suitable = Stage 2+3+4 (n = 4,903). Unsuitable = Stage 1+5 (n = 2,530). Absent = Stage 0 (n = 576).
Date of last pruning	Old (>10 yrs). Medium (5-10 yrs). Recent (< 5 yrs). Missing data (n = 9).	Old (n = 5,369). Medium (n = 1,605). Recent (n = 1,031).
Crown development	Absence of crown either because tree is dead or after a recent, major pruning (n = 351). Small crown (n = 810). Medium crown (n = 1,700). Large crown (n = 1,975). Very large crown (n = 3,170). Missing data (n = 8).	Absent or small (n = 1,161). Medium size = Medium + large (n = 3,675). Very large (n = 3,170).
Presence of <i>Osmoderma eremita</i>	Observation of larvae, adults, exoskeleton remains and/or faecal pellets of larvae of <i>O. eremita</i> .	Presence (n = 42). Absence (n = 7,972).
Distance to the nearest tree inhabited by <i>Osmoderma eremita</i>	Minimum distance, in metres, to the nearest tree with presence of <i>O. eremita</i> , calculated after GPS coordinates of the trees.	Metric.
Length of TOW per 1km ²	Length of hedgerow with trees per square of a 1km ² grid.	Metric: Min.: 0.0; Median: 2,616; Mean: 2,844; Max.: 7,768.

Ranges of 1km² and 250m were chosen because they corresponded respectively to the average dispersal distances already published for *O. eremita* (see above), as well as to infrequent but longer dispersal distances.

Data analysis

To find the variables that significantly affect the occurrence of *O. eremita*, two techniques were used. First, univariate analyses were used to assess each variable independently against occurrence of *O. eremita*. Second, generalised linear models (GLMs) were run with a binomial error distribution and logit link function. One important weakness of GLMs is that they consider the absence data to be certain. However, it is clear that the detection probability of *O. eremita* in wood mould sampling is well below 100% (Chiari et al. 2014, see discussion). Models were compared using Akaike's information criterion (AIC). The AIC value was calculated as $-2 \times \log\text{-likelihood} + k \times \text{npar}$, where npar represents the number of parameters in the fitted model and $k = 2$ (Burnham and Anderson 2004). The best model which minimises the overall AIC, was retained by means of a stepwise model selection by AIC (stepAIC), available in the MASS package of the R software.

Means of the data issued from TOW measurements in the 1km² grid were compared using one-way ANOVA. Correlations were explored with the non-parametric Spearman's rank correlations.

All statistical analyses and models were carried out with the R software version 3.1.0, RStudio version 0.99.896 and PAST version 2.17c (Hammer 2012). Mapping and calculation of spatial data were carried out with the software QGIS version 2.16.2.

Results

Temporal changes in the hedgerow network: 1973–2009

The PNR-BSN comprises 900 squares of 1km², inside of which 70,616 hedgerows and TOW have been mapped, for a total length of 3,898km according to the most recent analysis based on the aerial photographs from 2009. TOW represented 1,258.6km, a number that includes 151.2km of discontinuous hedgerow with trees and at least 5.4km of pollards in rows (pollards were not identified everywhere).

From 1973 to 2009, an increase of the total length of hedge length was found: +30.9% between 1973 and 1999 and +6.2% between 1999 and 2009 (Figure 1). These results might suggest a satisfactory situation but it is also true that 875km of hedges that had existed in 1973 were absent in 2009 (all types). The length of TOW diminished by 6.1% from 1999 to 2009. Hedges created between 1999 and 2009 were mostly low hedges composed of bushes. These were mostly concentrated around newly urbanised areas and are clearly unsuitable for *Osmoderma*. Plantation and tree re-growth represented 1,117km of young trees in 1999, reaching 1,341km in 2009 (+20.1%). These young trees are still mostly without cavities.

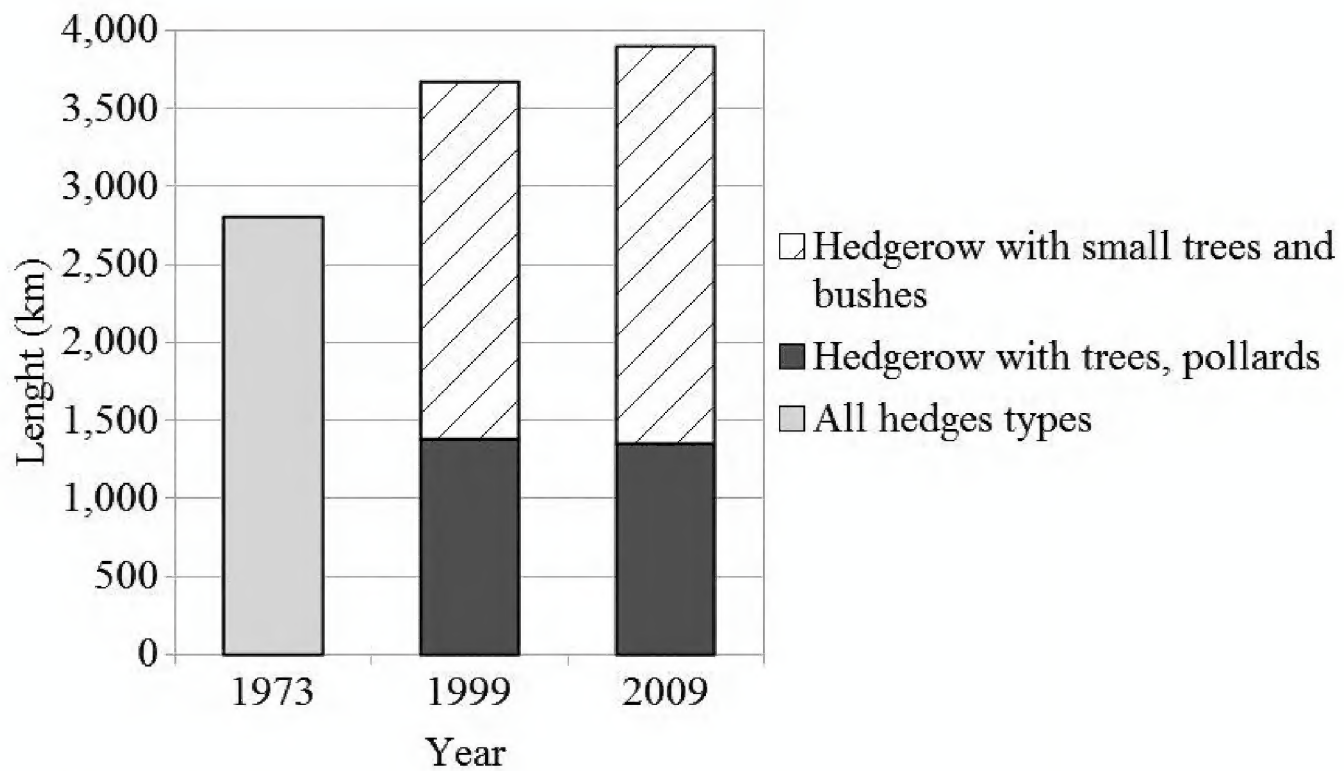


Figure 1. Temporal changes of the hedgerow network in the PNR-BSN.

Occurrence of *Osmoderma eremita*

Of the 8,014 trees studied, 4,903 (61%) presented a cavity suitable for *O. eremita* and 42 were identified as being inhabited by *O. eremita*. Four trees hosted live adults; the others contained adult remains and/or faecal pellets of larvae. The data indicated a hermit beetle population mostly confined along the meander of Jumièges, Anneville/Ambourville and Roumare.

The surveys recorded a majority of trees belonging to *Salix*, *Fraxinus* and *Populus*. *O. eremita* was clearly abundant in *Salix*, with 30 inhabited trees identified. However, the ratio between the numbers of trees surveyed versus trees inhabited by *O. eremita* was highest for *Quercus*, with 4.05% of the trees inhabited. In contrast, this value was lower for *Salix* (0.76%) and even lower for *Fraxinus* (0.22%).

Most of the willows had been pruned and developed a suitable cavity in 74.6% of cases, a ratio which represents a higher percentage of possessing a cavity when compared to ash (51.6% of trees with cavities) and poplars (37.0% of trees with cavities) (Table 3).

Habitat description

The best fitting GLM (AIC = 426.39) identified Tree genera, Developmental stage of the cavity, Crown development and Distance to the nearest tree inhabited by *O. eremita* as the most important variables. Date of last pruning and Length of TOW per 1km² were excluded during the selection process (Table 4).

Table 3. Count of inventoried trees according to the presence of suitable cavities and observations of *O. eremita*. †: refers exclusively to unidentified trees species.

Trees genera	Number of trees	Trees with cavities in stage 2, 3 and 4	Presence of <i>Osmoderma eremita</i> (% of the number of trees)
<i>Acer</i>	63	40	0
<i>Alnus</i>	63	53	2 (3.17%)
<i>Carpinus</i>	185	147	0
<i>Fraxinus</i>	2,227	1,149	5 (0.22%)
<i>Populus</i>	1,286	476	0
<i>Quercus</i>	74	29	3 (4.05%)
<i>Salix</i>	3,961	2,953	30 (0.76%)
<i>Tilia</i>	73	25	0
<i>Castanea</i> , <i>Crataegus</i> , <i>Malus</i> , <i>Ulmus</i> , etc., plus unidentified	82	31	2 (5.26%)†
Total	8,014	4,903	42

Table 4. Coefficients and probabilities associated with the variables of the best fitting GLM predicting the presence of *O. eremita*. Significance thresholds: 0.001 % (***), 0.01 % (**), not-significant (ns). GLM deviances: Null deviance = 524.79 on 8,004 degrees of freedom; Residual deviance = 408.39 on 7,996 degrees of freedom; AIC = 426.39.

Variables	Estimate	Standard error	z	Pr (> z)
All variables	-23.70	1,718	-0.014	0.98899
Tree genera - Other	2.143	0.5943	3.606	0.00031 ***
Tree genera - <i>Populus</i>	-13.71	974.9	-0.014	0.98878
Tree genera - <i>Salix</i>	1.353	0.4915	2.752	0.00592 **
Crown development - Medium	1.094	0.6221	1.759	0.07858
Crown development - Absent or small	2.016	0.6333	3.183	0.00146 **
Evolution stage of hollow - Suitable	17.38	1,718	0.010	0.99193
Evolution stage of hollow - Unsuitable	17.70	1,718	0.010	0.99178
Distance to the nearest tree inhabited by <i>Osmoderma eremita</i>	-0.001163	0.0003581	-3.248	0.00116 **

Spatial analysis: 250m buffer.

Significant values for the variables selected in the GLM involved trees other than *Fraxinus* and *Populus* and underlined the importance of *Salix*, inside of which most of the observations of *O. eremita* were made. A small crown or its absence also played a significant and positive role in the model. Finally, a greater distance to the nearest inhabited tree negatively affected the model.

TOW with a suitable cavity (thereafter named STOW), with a distance of less than 250m from other STOW, were distributed in the PNR-BSN within 75 areas disconnected from each another. Only a few of these areas were wide and included many STOW, whereas all other areas were small and included fewer STOW (Figure 2). As expected, the number of STOW was correlated with the surface of the areas (Spear-

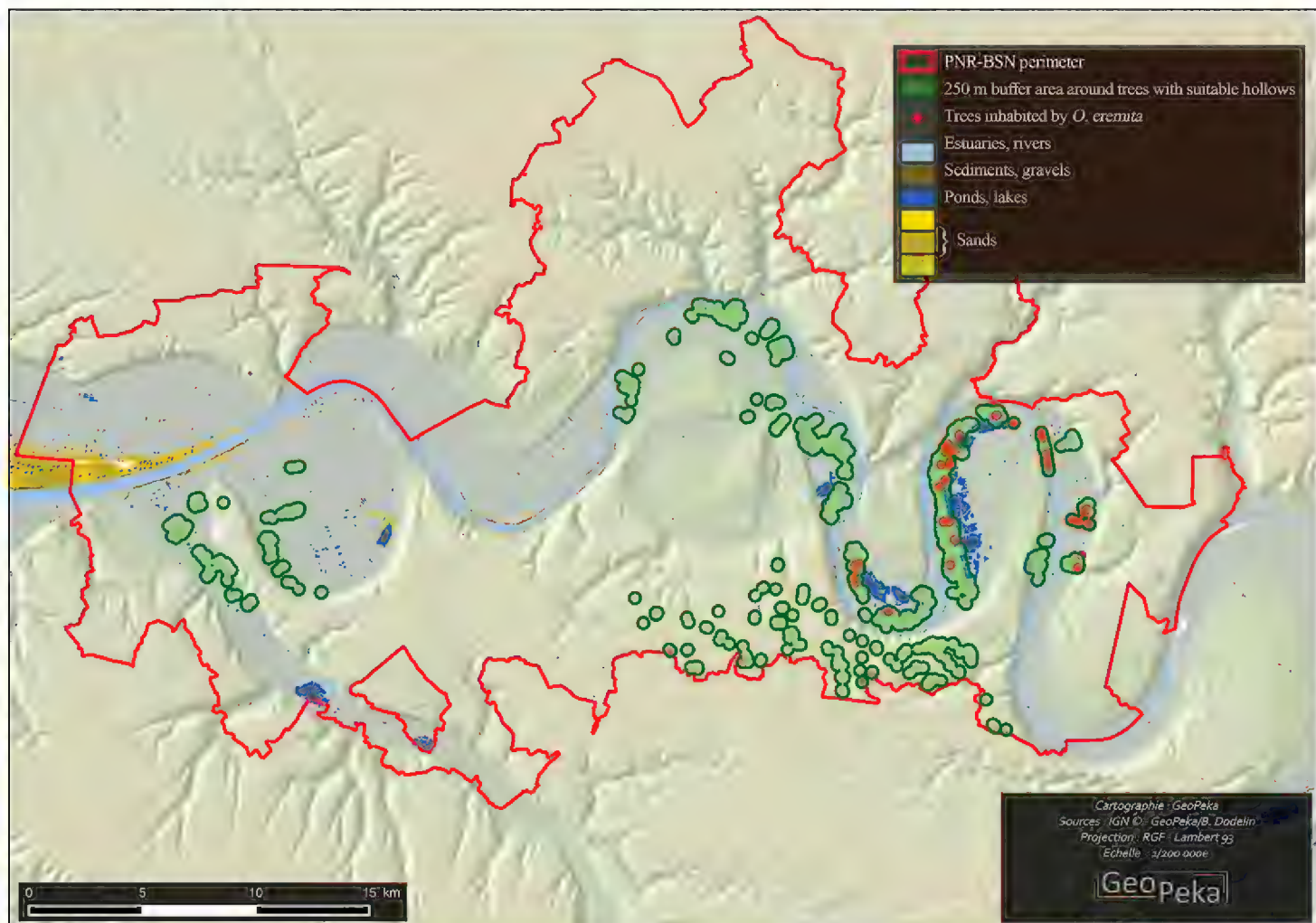


Figure 2. Distribution map of inhabited trees in the PNR-BSN according to the TOW length in each 1km² square. Spatial analysis: 1km² grid.

man's $D = 0.874660$, $p < 0.0001$) and ranged from 0.05 STOW/ha to 4.14 STOW/ha. The largest area (843.68ha) included the highest number of STOW (2,072) but not the highest density (2.46 STOW/ha). In this area, the highest number of trees inhabited by *O. eremita* ($n = 19$) had been found. Only one inhabited tree was found in each of four areas, five inhabited trees in one area and seven inhabited trees were discovered in two areas (range: 0.05 STOW/ha to 2.22 STOW/ha).

Only 96 squares from a total of 900 were included in the tree inventory. These represented 238km of TOW (19% of the total length). Trees inhabited by *O. eremita* belonged to 17 squares, including 63km of TOW (5% of the total length) (Table 5). Hedgerow lengths reported in the sub-sample of inventoried squares were significantly different from the total (ANOVA: $Q = 5.847$; $p = 0.0001233^{***}$). The sampling protocol introduced a bias in favour of squares with the highest length of TOW (on average 177% of the whole average length). However, the squares with presence of *O. eremita* contained significantly more TOW than other squares investigated (ANOVA: $Q = 6.574$; $p < 0.0001^{***}$), respectively 3.69km and 2.48km, in comparison with 1.40km for the PNR-BSN. As a consequence, squares inhabited by *Osmoderma* contained 2.5 times more TOW than the average in the PNR-BSN (Figure 3).

With the GIS system, it was possible to identify squares with a total length of TOW equal to or greater than that of the squares with trees inhabited by *O. eremita*.

Table 5. Lengths of TOW in the 1km² squares of the PNR-BSN. Data from 2009.

Data per square	PNR-BSN (n = 900 squares)	Sampled trees (n = 96 squares)	Trees inhabited by <i>O. eremita</i> (n = 17 squares)
TOW length (km)	1,340.90	238.00	62.66
Average length (km) of TOW	1.40	2.48	3.69
Median length (km) of TOW	1.19	2.27	3.86

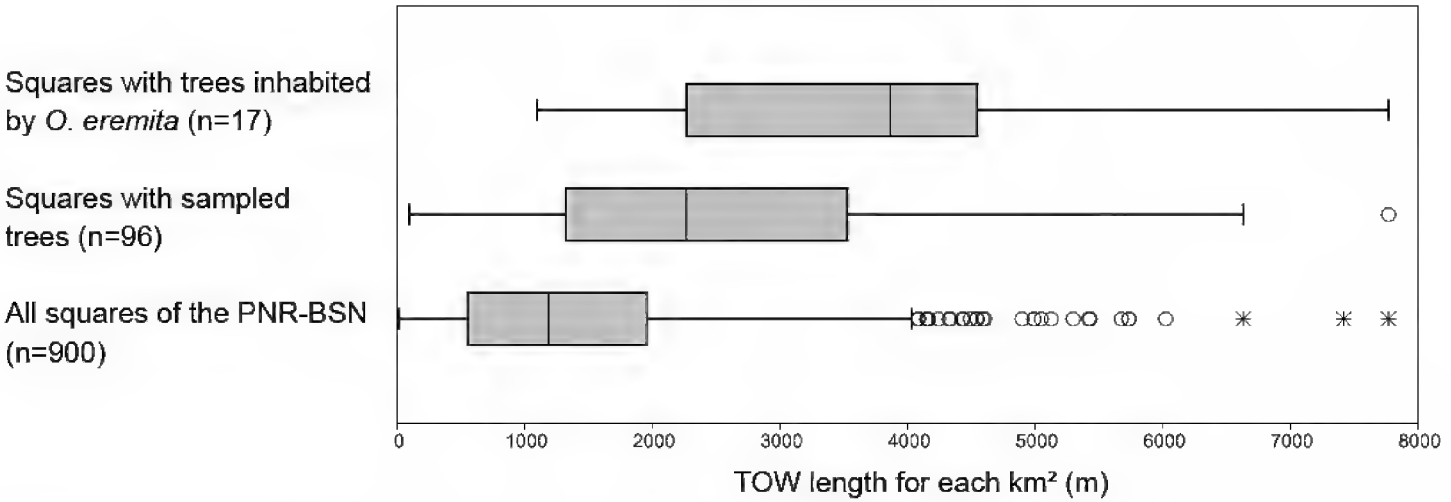


Figure 3. Frequencies of 1km² squares according to the TOW length. Three sample groups are presented: PNR-BSN (n = 900 squares); Sampled trees (n = 96 squares); Trees inhabited by *O. eremita* (n = 17 squares). All differences between groups are significant at the threshold of 0.001% (ANOVA).

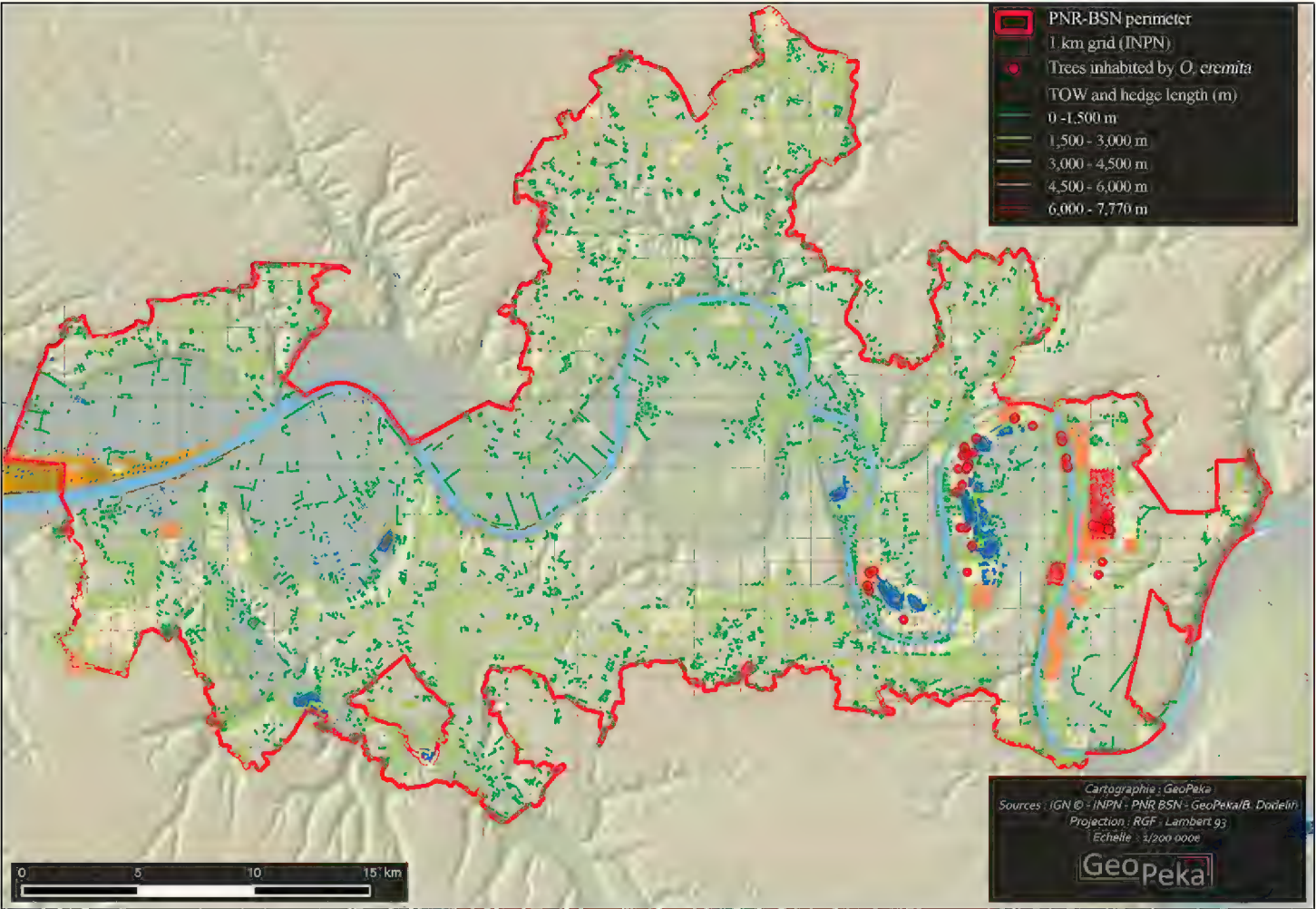


Figure 4. Distribution map of the TOW and hedges in the PNR-BSN indicating the TOW length in each 1km² square.

In this manner, two large areas were delimited which may have been occupied by the hermit beetle i.e. the meander of Roumare, in the west of the city of Canteleu and the lower part of the Risle valley, plus the plateau of Saint-Pierre-du-Val (Figure 4).

Discussion

Habitat characteristics

Osmoderma species are known to live in the cavities of many tree species: *Quercus* (many studies), *Tilia* and *Alnus* (Oleksa et al. 2007), *Castanea* (Macagno et al. 2012, Chittaro and Morin 2013), *Fagus* (Tauzin 2005) and others (for a more complete list, see e.g. Ranius et al. 2005). Landvik et al. (2016b) considered the species to be opportunistic with respect to their host trees. On the other hand, *Fraxinus* and *Acer* seem to be avoided by the hermit beetle even in locations where they are abundant (Oleksa et al. 2007, Dubois et al. 2009, Kadej et al. 2016). The heartwood of those trees is rarely colonised by red-rot fungi and thus cavities suitable for *O. eremita* are not created. In contrast, the data from the study showed that willows can be key species when they are abundant (see also Sebek 2008) and this finding is important from a conservation point of view. However, the rate of occupancy in this study was in line with most of the previous studies in that it was higher for oaks (4.05%) and lower for willows (0.76%) and ash (0.22%).

The GLM model used showed a weakness as it considered absence data to be certain. This is unrealistic with *Osmoderma*, as it is a “hard-to-find” species in many situations (Chiari et al. 2014). A solution to minimise the impact of “false absences” in the occupancy modelling is to repeat surveys at a site, or in multiple sub-sites, in order to estimate species detection probabilities. This detection might fit the ‘closure’ (i.e. no changes in occupancy) assumption between surveys (Rota et al. 2009, Kendall et al. 2013). Violations of closure typically lead to overestimates of the probability of occurrence (Rota et al. 2009). After multiples surveys, the obtained probability of species presence can be added as a simple probabilistic argument in the occupancy models (MacKenzie et al. 2002, Tyre et al. 2003, MacKenzie 2005). Another solution is to consider background data. Background data establish the environmental domain where the species can be more likely present than on average. They can include or reflect the sampling bias (Phillips et al. 2009) which can be added in regression-based modelling methods such as MaxEnt (Dudík et al. 2005).

In this study, the used model indicated that the date of last pruning was irrelevant but showed that a small or absent crown was a significant factor. As, in most cases, pruning is the main cause for a reduced size or an absence of canopy, this result seems incongruous at first. Moreover, in an agricultural landscape, willows had generally been pollarded to avoid the growth of large branches subject to breakage over the medium term (Juillerat and Vögeli 2004). The significance of small crowns in the model may therefore have resulted from the predominant presence of *Salix* in our data,

though it is also clearly obvious that tree species and crown size are not correlated. Consequently, the three categories used to assess the date of last pruning, based on markers at 5 and 10 years, may ultimately be too narrow to provide reliable information about the development of suitable conditions for the hermit beetle. In a way, crown size better correlates with this parameter, as it integrates old pruning and the resulting long process of cavity formation. The time scale of 5 and 10 years had been chosen for practical reasons, to prioritise trees in need of pruning.

TOW density and *O. eremita* presence

Inhabited trees were found to be more abundant in the larger areas established by applying a 250m buffer zone around any TOW with a suitable cavity. No link with the density of hollow trees per ha was however found. The areas with the highest densities of STOW were searched without success. The observed densities in areas with *O. eremita* were at most 2.46 STOW/ha. Ranius et al. (2011) suggested a density of 0.69 hollow oaks per ha within a radius of 192m to ensure the presence of two cavity-specialist arthropods. In this study, densities of hollow trees were higher in most areas, corresponding better to the situation studied by Hedin et al. (2008) (1.4 to 4.3 hollow tree/ha) or indicated by Tauzin (2005) in Fontainebleau (1.6 hollow tree/ha) and Vignon and Orabi (2003) in the Mayenne and Sarthe departments (1.4 hollow tree/ha). Dubois et al. (2009) also found a better response by *O. eremita* to lower densities, close to 1 hollow tree/ha, than to higher ones (1.4 hollow tree/ha). Open landscapes thus seem to be crucial for *O. eremita* in northern Europe (Ranius and Jansson 2000, Landvik et al. 2016b), whereas it is less so in a Mediterranean climate (Chiari et al. 2012). Several other factors may also be important to explain the observed patterns: low detectability (false absences), environmental factors (unsuitable cavities, dispersal difficulties in dense canopy conditions (e.g. Dubois and Vignon 2008)) and historical factors (ancient local extinction without re-establishment).

Conclusion and implication for the conservation of *O. eremita*

This study confirmed the presence in the PNR-BSN of the endangered and highly specialised saproxylic beetle *O. eremita*. This confirmation was often based only on traces of its presence, but also on live specimens. It seems likely that *O. eremita* survived because the landscape of the studied area had not dramatically changed. Moreover, this area benefited from a favourable situation with about 10 times more suitable hollow trees than observed in a nearby site which comprised similar numbers of trees surveyed and trees inhabited by *O. eremita* (Dubois et al. 2009).

This study also showed that the length of TOW existing in 1999 had decreased by 6.1% in 2009. Thus, if no protection measures are undertaken, the long term survival of *O. eremita* in the PNR-BSN is under threat. In the upper Elbe valley,

Lorenz (2013) described a decrease of suitable trees of approximately 3% to 5% per year. This decline is higher than the annual mortality rates given by Drobyshev et al. (2008) of about 1% for oak populations located outside dense forests. At a rate of 3%, it would take only 10 to 15 years to lose a quantity of TOW comparable to that which was observed between 1973 and 2009. If the decline continues, Lorenz estimated that *O. eremita* may seriously decline and eventually become extinct in the next 40 years (Lorenz 2013). Although the situation appeared more favourable in the PNR-BSN, it will take decades before young trees develop cavities to replace the existing ones. Therefore, policies and actions must be decided rapidly and with the long term perspective in mind (>150 years).

An action plan for the preservation of old trees is already in progress in the PNR-BSN. It includes several approaches: financial help for pruning, a dedicated commission, an awareness campaign for the public and schools, a reflection on the economic role of pollarded trees in relation to firewood and, wherever possible, an integration of measures for the conservation of pollarded trees into urban planning documents. This is in agreement with the proposal of Stegner (2002), for the conservation of the hermit beetle in Saxony, to include monitoring, direct protection and publicity efforts. Regeneration and creations of new TOW are priorities and are ongoing in the PNR-BSN, mainly inside protected areas and in the Natura 2000 network. Between 2005 and 2013, 2,174 trees have been planted and about 2,000 have been pruned with the help of the PNR-BSN (Coppée et al. 2016). Management of existing trees by pollarding is to be favoured to enhance the formation of cavities (Messerschmidt and Schmidl 2015). Willows can play a key role in this respect as they grow fast and are quickly colonised by heart-rot fungi, even when young. As their life-spans are generally short, ten times less than oaks (Otto 1998), they must be pruned in order to survive for adequate periods of time (Juillerat and Vögeli 2004). After pruning, they develop cavities faster than hardwood trees. With regards to oaks, Ranius et al. (2009) described a very slow process, with about 200–300 years required for 50% of trees to develop cavities and 400 years are required for all oaks to develop cavities. In a study on *Salix alba*, Sebek et al. (2013) found a probability of cavity formation of approximately 80% in pollards with a diameter of 30-60cm, but only approximately 30% of non-pollards of the same diameter class developed cavities. On the landscape scale, Kirby (2015) suggested a model of regeneration as a series of episodic events, rather than a continuous recruitment of young trees. This strategy would lead to cohorts of different ages that will neither compete with existing trees nor modify the character of the site. This makes it possible to focus work on small areas with greater efficiency.

In the medium term, it is important to work to establish *O. eremita* as a flagship species for the public, even if this status will not necessarily confer protection to all other taxa associated with the flagship species (Roberge and Angelstam 2004). Moreover, Sebek et al. (2012) were unable to find clear evidence that saproxylic beetles are positively related to the presence of *O. barnabita*. This association would appear to occur rather as a function of the cavity parameters (Micó et al. 2015) or at the tree and stand levels, especially in relation to the sunlight conditions (Horák et al. 2014, Sebek et al. 2016, Parmain and

Bouget 2017). Many indicators strongly suggest that veteran trees hosting *Osmoderma* are also inhabited by remarkable and highly diverse saproxylic beetle populations (Ranius 2002, Chittaro and Sanchez 2015). With the help of *O. eremita* as a flagship species, it appears possible to reconnect landowners to their veteran trees which are also witnesses of ancient practices and cultural heritage (Blanc 2012, Hartel and Plieninger 2014).

Acknowledgements

We would like to thank all the people involved in this work, especially Elodie Brunet, Amélie Garcia-Chaib, Jaime Jimenez, Nicolas Moulin, Mégane Skrzyniarz, Lionel Valladares, Vincent Vignon. We are also grateful to Gaëlle Darmon for her help with statistics and modelling, to Keith Alexander and to the two referees for their relevant remarks and suggestions for improvement of our initial submission. This study was funded by the DREAL Normandie, the Normandie region and "l'Eau Seine Normandie" agency.



Special issue published with the contribution of the LIFE financial instrument of the European Union.

References

- Alexander KNA (2008) Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. *Revue d'Ecologie, Terre Vie*, 63: 1–7.
- Alexander KNA, Bengtsson VJ, Jansson N, Smith JP (2016) The role of trees outside woodlands in providing habitat and ecological networks for saproxylic invertebrates. Part 1 Designing a field study to test initial hypotheses. *Natural England*, Worcester, 1–111. <http://publications.naturalengland.org.uk/publication/4828234842112000>
- ALISE Environnement, Moulin N, Université de Rouen (2008) Étude des populations de Pique-prune (*Osmoderma eremita*) sur la partie ouest du Parc naturel régional des Boucles de la Seine normande. Rapport du bureau d'étude ALISE Environnement pour le Parc naturel régional des Boucles de la Seine normande, Saint-Jacques-sur-Darnétal, 1–39.
- Audisio P, Brustel H, Carpaneto GM, Coletti G, Mancini E, Piattella E, Trizzino M, Duttto M, Antonini G, De Biase A (2007) Updating the taxonomy and distribution of the European *Osmoderma*, and strategies for their conservation (Coleoptera, Scarabaeidae, Cetoniinae). *Fragmenta entomologica* 39: 273–290. <https://doi.org/10.4081/fe.2007.124>
- Audisio P, Brustel H, Carpaneto GM, Coletti G, Mancini E, Trizzino M, Antonini G, De Biase A (2009) Data on molecular taxonomy and genetic diversification of the European Hermit beetles, a species complex of endangered insects (Coleoptera: Scarabaeidae, Cetoniinae, *Osmoderma*). *Journal of Zoological Systematics and Evolutionary Research* 47: 88–95. <https://doi.org/10.1111/j.1439-0469.2008.00475.x>

- Bensettiti F, Puissauve R (2015) Résultats de l'état de conservation des habitats et des espèces dans le cadre de la directive Habitats-Faune-Flore en France. Service du patrimoine naturel, Muséum national d'histoire naturelle, Paris, 204 pp.
- Blanc M (2012) A propos d'*Osmoderma eremita* (Scopoli, 1763) en Suisse. *Schweizerische Zeitschrift für Forstwesen* 163: 271–276. <https://doi.org/10.3188/szf.2012.0271>
- Burel F, Baudry J (1990) Structural dynamic of a hedgerow network landscape in Brittany France. *Landscape ecology* 4: 197–210. <https://doi.org/10.1007/BF00129828>
- Burel F, Butet A, Delettre YR, Millàn de la Peña N (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning* 67: 195–204. [https://doi.org/10.1016/S0169-2046\(03\)00039-2](https://doi.org/10.1016/S0169-2046(03)00039-2)
- Burnham KP, Anderson DR (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research* 33: 261–304. <https://doi.org/10.1177/0049124104268644>
- Buse J, Entling MH, Ranius T, Assmann T (2016) Response of saproxylic beetles to small-scale habitat connectivity depends on trophic levels. *Landscape Ecology* 31: 939–949. <https://doi.org/10.1007/s10980-015-0309-y>
- Chiari S, Carpaneto GM, Zauli A, Marini L, Audisio P, Ranius T (2012) Habitat of an endangered saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Ecoscience* 19: 299–307. <https://doi.org/10.2980/19-4-3505>
- Chiari S, Carpaneto GM, Zauli A, Zirpoli GM, Audisio P, Ranius T (2013) Dispersal patterns of a saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. *Insect Conservation and Diversity* 6: 309–318. <https://doi.org/10.1111/j.1752-4598.2012.00215.x>
- Chiari S, Zauli A, Audisio P, Carpaneto GM (2014) Interactions between larvae of the threatened saproxylic beetle *Osmoderma eremita* and other flower chafers in Mediterranean woodlands: implications for conservation. *Insect Conservation and Diversity* 7(5): 462–469. <https://doi.org/10.1111/icad.12069>
- Chittaro Y, Morin C (2013) Redécouverte d'*Osmoderma eremita* (Scopoli, 1763) en Valais (Coleoptera, Scarabaeidae, Cetoniinae). *Entomo Helvetica* 6: 165–167.
- Chittaro Y, Sanchez A (2015) Inventaire des coléoptères saproxyliques d'un site exceptionnel: la châtaigneraie de Fully (VS). *Bulletin Murithienne* 133: 13–27.
- Coppée J-L, De Mori H, Noiret C (2016) Le Saule - Roi des têtards. *Les Bocages* (Couvin): 1–384. Available from: <http://www.lesbocages.be/>.
- Dirksen T, Mériguet B (2009) *Osmoderma eremita* dans l'Yonne: une nouvelle station menacée (Coleoptera; Cetoniidae). *L'Entomologiste* 65: 55–59.
- Drobyshev I, Niklasson M, Linderson H, Sonesson K, Karlsson M, Nilsson SG, Lanner J (2008) Lifespan and mortality of old oaks—combining empirical and modelling approaches to support their management in Southern Sweden. *Annals of forest science* 65: 1–12. <http://dx.doi.org/10.1051/forest:2008012>
- Dubois G (2009) Écologie des coléoptères saproxyliques: Biologie des populations et conservation d'*Osmoderma eremita* (Coleoptera: Cetoniidae). Université de Rennes 1.
- Dubois G, Le Gouar PJ, Delettre YR, Brustel H, Vernon P (2010) Sex-biased and body condition dependent dispersal capacity in the endangered saproxylic beetle *Osmoderma er-*

- emita* (Coleoptera: Cetoniidae). Journal of Insect Conservation 14: 679–687. doi:10.1007/s10841-010-9296-0
- Dubois G, Vignon V (2008) First results of radio-tracking of *Osmoderma eremita* (Coleoptera: Cetoniidae) in French chestnut orchards. Revue d'écologie: 131–138.
- Dubois G, Vignon V, Delettre YR, Rantier Y, Vernon P, Burel F (2009) Factors affecting the occurrence of the endangered saproxylic beetle *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. Landscape and Urban Planning 91: 152–159. doi:10.1016/j.landurbplan.2008.12.009
- Dudík M, Schapire RE, Phillips SJ (2005) Correcting sample selection bias in maximum entropy density estimation. In: Advances in neural information processing systems. Weiss Y, Schölkopf PB, Platt JC, Cambridge, Massachusetts, USA, 323–330.
- Fayt P, Dufrêne M, Branquart E, Hastir P, Pontégnie C, Henin J-M, Versteirt V (2006) Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests. Journal of Insect Conservation 10: 129–150. <https://doi.org/10.1007/s10841-006-6289-0>
- Gaudet S (2013) Le Pique prune (*Osmoderma eremita*, Scopoli 1763) en vallée de Seine: Stratégie de conservation 2012-2016. Parc naturel régional des Boucles de la Seine Normande, Notre-Dame-de-Bliquetuit, 1–67.
- Hammer Ø (2012) PAST - PAleontological STatistics, version 2.14. Reference manual. Natural History Museum & University of Oslo, Oslo, 1–225.
- Hartel T, Plieninger T (2014) European wood-pastures in transition: A social-ecological approach. Routledge, London, 1–303.
- Hedin J, Ranius T, Nilsson SG, Smith HG (2008) Restricted dispersal in a flying beetle assessed by telemetry. Biodiversity and Conservation 17: 675–684. <https://doi.org/10.1007/s10531-007-9299-7>
- Horák J, Vodka S, Kout J, Halda JP, Bogusch P, Pech P (2014) Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. Forest Ecology and Management 315: 80–85. <https://doi.org/10.1016/j.foreco.2013.12.018>
- Juillerat L, Vögeli M (2004) Gestion des vieux arbres et maintien des Coléoptères saproxyliques en zone urbaine et périurbaine. Centre Suisse de Cartographie de la Faune, Neuchâtel, 1–21. Available from: http://ge.ch/nature/media/nature/files/fichiers/documents/gestion_vieux_arbres_et_maintien_coleopteres_saproxyliques.pdf
- Kadej M, Zając K, Smolis A, Tarnawski D, Malkiewicz A (2016) Isolation from forest habitats reduces chances of the presence of *Osmoderma eremita sensu lato* (Coleoptera, Scarabaeidae) in rural avenues. Journal of Insect Conservation 20: 395–406. <https://doi.org/10.1007/s10841-016-9873-y>
- Kendall WL, Hines JE, Nichols JD, Grant EHC (2013) Relaxing the closure assumption in occupancy models: staggered arrival and departure times. Ecology 94: 610–617. <https://doi.org/10.1890/12-1720.1>
- Kirby KJ (2015) What Might a Sustainable Population of Trees in Wood-Pasture Sites Look Like? Hacquetia 14. <https://doi.org/10.1515/hacq-2015-0010>

- Landvik M, Wahlberg N, Roslin T (2013) The identity of the Finnish *Osmoderma* (Coleoptera: Scarabaeidae, Cetoniinae) population established by COI sequencing. *Entomologica Fennica* 24: 147–155.
- Landvik M, Niemelä P, Roslin T (2016a) Mother knows the best mould: an essential role for non-wood dietary components in the life cycle of a saproxylic scarab beetle. *Oecologia* 182: 163–175. <https://doi.org/10.1007/s00442-016-3661-y>
- Landvik M, Niemelä P, Roslin T (2016b) Opportunistic habitat use by *Osmoderma barnabita* (Coleoptera: Scarabaeidae), a saproxylic beetle dependent on tree cavities. *Insect Conservation and Diversity* 9: 38–48. <https://doi.org/10.1111/icad.12141>
- Larsson MC, Hedin J, Svensson GP, Tolasch T, Francke W (2003) Characteristic odor of *Osmoderma eremita* identified as a male-released pheromone. *Journal of Chemical Ecology* 29: 575–587. <https://doi.org/10.1023/A:1022850704500>
- Lorenz J (2013) Historische Nachweise, gegenwärtige und Prognose der zu-künftigen Bestandssituation des Eremiten (*Osmoderma eremita* (Scopoli, 1763)) in Sachsen (Coleoptera: Scarabaeidae). *Sächsische Entomologische Zeitschrift* 7: 3–29.
- Luce J-M (1995) Écologie des Cétoines (Coleoptera : Cetoniidae) micro-cavernicoles de la Forêt de Fontainebleau : niches écologiques, relations interspécifiques et conditions de conservation des populations. PHD Thesis. Muséum National d'Histoire Naturelle, Paris.
- Luce J-M (2001) La cétoine protégée *Osmoderma eremita* (Scopoli, 1763) peut-elle être un outil de gestion de la biodiversité ? In: Actes du séminaire tenu à Besançon les 8, 9 et 10 juillet 1999. MNHN Paris, service patrimoine naturel & OPIE, Paris, 243–263.
- Macagno AL, Gobbi M, Franceschini A, Lencioni V (2012) New record of *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) in chestnut trees in Trentino (Eastern Italian Alps). *Studi Trentini di Scienze Naturali* 92: 37–41.
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83: 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- MacKenzie DI (2005) Was it there? Dealing with imperfect detection for species presence/absence data. *Australian & New Zealand Journal of Statistics* 47: 65–74. <https://doi.org/10.1111/j.1467-842X.2005.00372.x>
- MEDDE (2012) Stratégie nationale pour la biodiversité 2011–2020. <http://www.developpement-durable.gouv.fr/Strategie-nationale-pour-la>, 22931.html
- Messerschmidt D, Schmidl J (2015) Dreijahres-Monitoring von Brutbäumen (Kopfeichen) des Eremiten (*Osmoderma eremita* (Scopoli, 1763)) am Hetzleser Berg, Lkr. Forchheim, Nordbayern (Insecta: Coleoptera: Scarabaeidae). *Beiträge zur bayerischen Entomofaunistik* 15: 81–94.
- Micó E, García-López A, Sánchez A, Juárez M, Galante E (2015) What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity? *Journal of Insect Conservation*. <https://doi.org/10.1007/s10841-015-9754-9>
- Moilanen A, Nieminen M (2002) Simple Connectivity Measures in Spatial Ecology. *Ecology* 83: 1131–1145. [https://doi.org/10.1890/0012-9658\(2002\)083\[1131:SCMISE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1131:SCMISE]2.0.CO;2)

- Müller J, Bußler H, Bense U, Brustel H, Flechtner G, Fowles A, Kahlen M, Möller G, Mühle H, Schmidl J, Zabransky P (2005) Urwald relict species – Saproxylic beetles indicating structural qualities and habitat tradition. *Waldökologie online* 2: 106–113.
- Muséum national d'Histoire naturelle (2003) *Osmoderma eremita* (Scopoli, 1763). Inventaire National du Patrimoine Naturel. Available from: https://inpn.mnhn.fr/espece/cd_nom/10979 [February 7, 2017]
- Nieto A, Mannerkoski I, Putschkov A, Tykarski P, Mason F, Dodelin B, Tezcan S (2010) *Osmoderma eremita*. Available from: <http://www.iucnredlist.org/details/full/15632/0> [January 23, 2017]
- Oleksa A, Ulrich W, Gawronski R (2007) Host tree preferences of hermit beetles (*Osmoderma eremita* Scop., Coleoptera: Scarabaeidae) in a network of rural avenues in Poland. *Polish Journal of Ecology* 55: 315–323.
- Oleksa A, Chybicki IJ, Gawroński R, Svensson GP, Burczyk J (2013) Isolation by distance in saproxylic beetles may increase with niche specialization. *Journal of Insect Conservation* 17: 219–233. <https://doi.org/10.1007/s10841-012-9499-7>
- Otto HJ (1998) Écologie forestière. Institut pour le Développement Forestier, Paris, 1–397.
- Parmain G, Bouget C (2017) Large solitary oaks as keystone structures for saproxylic beetles in European agricultural landscapes. *Insect Conservation and Diversity*: 1–16. <https://doi.org/10.1111/icad.12234>
- Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19: 181–197. <https://doi.org/10.1890/07-2153.1>
- Prugh LR (2009) An evaluation of patch connectivity measures. *Ecological Applications* 19: 1300–1310. <https://doi.org/10.1890/08-1524.1>
- Ramírez-Hernández A, Micó E, Marcos-García M de los Á, Brustel H, Galante E (2014) The “dehesa”, a key ecosystem in maintaining the diversity of Mediterranean saproxylic insects (Coleoptera and Diptera: Syrphidae). *Biodiversity and Conservation* 23: 2069–2086. <https://doi.org/10.1007/s10531-014-0705-7>
- Ranius T (2002) *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. *Biodiversity and Conservation* 11: 931–941. <https://doi.org/10.1023/A:1015364020043>
- Ranius T, Aguado LO, Antonsson K, Audisio P, Ballerio A, Carpaneto GM, Chobot K, Gjurašin B, Hanssen O, Huijbregts H, Lakatos F, Martin O, Neculiseanu Z, Nikitsky NB, Paill W, Pirnat A, Rizun V, Ruicanescu A, Stegner J, Süda I, Szwalko P, Tamutis V, Telnov D, Tsinkevich V, Versteirt V, Vignon V, Vögeli M, Zach P (2005) *Osmoderma eremita* (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. *Animal Biodiversity and Conservation* 28: 1–44.
- Ranius T, Antonsson K, Jansson N, Johannesson J (2001) Inventering och skötsel av gamla ekar i Eklandskapet söder om Linköping [Inventories and management of old oaks in an area south of Linköping, Sweden]. *Fauna och Flora* 96: 97–107. <https://doi.org/10.1007/s004420000529>
- Ranius T, Hedin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* 126: 363–370.

- Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation* 95: 85–94. [https://doi.org/10.1016/S0006-3207\(00\)00007-0](https://doi.org/10.1016/S0006-3207(00)00007-0)
- Ranius T, Jansson N (2002) A comparison of three methods to survey saproxylic beetles in hollow oaks. *Biodiversity and Conservation* 11: 1759–1771. <https://doi.org/10.1023/A:1020343030085>
- Ranius T, Johansson V, Fahrig L (2010) A comparison of patch connectivity measures using data on invertebrates in hollow oaks. *Ecography* 33: 971–978. <https://doi.org/10.1111/j.1600-0587.2009.06363.x>
- Ranius T, Johansson V, Fahrig L (2011) Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. *Biodiversity and Conservation* 20: 2027–2040. <https://doi.org/10.1007/s10531-011-0072-6>
- Ranius T, Niklasson M, Berg N (2009) Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management* 257: 303–310. <https://doi.org/10.1016/j.foreco.2008.09.007>
- Roberge JM, Angelstam P (2004) Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conservation Biology* 18: 76–85. <https://doi.org/10.1111/j.1523-1739.2004.00450.x>
- Rota CT, Fletcher Jr RJ, Dorazio RM, Betts MG (2009) Occupancy estimation and the closure assumption. *Journal of Applied Ecology* 46: 1173–1181. doi: <https://doi.org/10.1111/j.1365-2664.2009.01734.x>
- Sebek P (2008) The importance of pollard willows at the locality Vojkovická vrb ovna for the Hermit Beetle (*Osmoderma eremita*) and other beetles (Coleoptera) of tree cavities. PHD Thesis. Masarykova univerzita, (Brno).
- Sebek P, Cizek L, Hauck D, Schlaghamersky J (2012) Saproxylic beetles in an isolated pollard willow stand and their association with *Osmoderma barnabita* (Coleoptera: Scarabaeidae). In: Jurc M (Ed.) Saproxylic beetles in Europe: monitoring, biology and conservation. Studia Forestalia Slovenica, Ljubljana, 67–72.
- Sebek P, Altman J, Platek M, Cizek L (2013) Is Active Management the Key to the Conservation of Saproxylic Biodiversity? Pollarding Promotes the Formation of Tree Hollows. *PLoS ONE* 8: e60456. <https://doi.org/10.1371/journal.pone.0060456>
- Sebek P, Vodka S, Bogusch P, Pech P, Tropek R, Weiss M, Zimova K, Cizek L (2016) Open-grown trees as key habitats for arthropods in temperate woodlands: The diversity, composition, and conservation value of associated communities. *Forest Ecology and Management* 380: 172–181. <https://doi.org/10.1016/j.foreco.2016.08.052>
- Simont V, Dufrêne P (2007) Étude des populations de Pique-prune (*Osmoderma eremita*) sur le territoire du Parc régional des boucles de la Seine normande. Bureau d'étude ENERGI pour le Parc naturel régional des Boucles de la Seine normande, Cerisy-la-Salle, 1–51.
- Sparacio I (2000) Osservazioni sulle *Osmoderma* Le Peletier & Audinet-Serville europee con descrizione di una nuova specie dell'Italia meridionale (Col. Cetoniidae). *Il Naturalista siciliano* IV, XXIV: 225–239.
- Stegner J (2002) The Hermit-beetle *Osmoderma eremita* (Scopoli, 1763) (Col. Scarabaeidae) in Saxony: Required protective measures for a priority species in the sense of the habitats-directive. *Entomologische Nachrichten und Berichte* 46: 213–238.

- Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, Cambridge, 1–509. <https://doi.org/10.1017/cbo9781139025843>
- Svensson GP, Oleksa A, Gawroński R, Lassance J-M, Larsson MC (2009) Enantiomeric conservation of the male-produced sex pheromone facilitates monitoring of threatened European hermit beetles (*Osmoderma* spp.). *Entomologia Experimentalis et Applicata* 133: 276–282. <https://doi.org/10.1111/j.1570-7458.2009.00923.x>
- Tauzin P (2005) Ethology and distribution of the “hermit beetle” in France (Coleoptera Cetoniidae, Trichiinae, Osmodermatini). *Cetoniimania* 4: 131–153.
- Tyre AJ, Tenhumberg B, Field SA, Niejalke D, Parris KP, Possingham HP (2003) Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* 13: 1790–1801. <https://doi.org/10.1890/02-5078>
- Valainis U, Nitcis M, Aksjuta K, Barševskis A, Cibulskis R, Balalaikins M, Avgin SS (2015) Results of using pheromone-baited traps for investigations of *Osmoderma barnabita* Motschulsky, 1845 (Coleoptera: Scarabaeidae: Cetoniinae) in Latvia. *Baltic Journal of Coleopterology (Latvia)* 15: 37–45.
- Vallauri D, André J, Dodelin B, Eynard-Machet R, Rambaud D (2005) Bois mort et à cavités, une clé pour les forêts vivantes. Lavoisier, Paris, 1–405.
- Vignon V (2008) Comparing size of *Osmoderma eremita* populations and habitat quality in different French localities: conservation perspectives. *Revue d'écologie*: 123–129.
- Vignon V, Dubois G (2005) Recherche du pique-prune (*Osmoderma eremita*) sur le territoire du Parc Naturel Régional des Boucles de la Seine Normande. Office de Génie Ecologique pour le Parc naturel régional des Boucles de la Seine Normande, Saint-Maur-des-Fossés, 1–29.
- Vignon V, Orabi P (2003) Exploring the hedgerows network in the west of France for the conservation of saproxylic beetles (*Osmoderma eremita*, *Gnorimus variabilis*, *Lucanus cervus*, *Cerambyx cerdo*). In: Proceedings of the second pan-European conference on Saproxylic Beetles. People's Trust for Endangered Species, London, 36–38.
- Zauli A, Carpaneto GM, Chiari S, Mancini E, Nyabuga FN, Redolfi De Zan L, Romiti F, Sabbani S, Audisio PA, Hedenström E, Bologna MA, Svensson GP (2016) Assessing the taxonomic status of *Osmoderma cristinae* (Coleoptera: Scarabaeidae), endemic to Sicily, by genetic, morphological and pheromonal analyses. *Journal of Zoological Systematics and Evolutionary Research*: 54: 206–214. <https://doi.org/10.1111/jzs.12127>